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Initial response of riparian plant community structure to clearing of invasive alien plants in Kruger National Park, South Africa

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Abstract

Recovery of indigenous species subsequent to the clearing of invasive alien plants (IAPs) is crucial for ecosystem recovery to occur. However, cleared sites are often just left in the hope that revegetation will occur naturally. In riparian areas of Kruger National Park (KNP), the Working for Water (WfW) Programme has cleared IAPs on a regular basis, but little post-clearance monitoring has taken place. Thus investigating short-term effects of IAPs and IAP clearing on plant community diversity and vegetation recovery provided an ideal opportunity to assess feasible targets of natural ecosystem recovery in similar areas. Vegetation was sampled from twelve transects along the Sabie River in and adjacent to the KNP, before (March/April 2006) and after (March 2007) the annual clearing of IAPs by WfW. Rarefied species richness, alpha diversity and evenness of distribution of species all declined with increasing density of IAPs ($P<0.05$). There was a mean reduction in IAP density of 80% (S.E±6%) ($P=0.002$) through the clearing by WfW. After clearing of IAPs, indigenous vegetation densities increased, with herbaceous growth forms showing the largest increase in transects that were previously heavily invaded. Thus, in this system, which is relatively undisturbed by human activities, initial recovery of indigenous vegetation can occur without further restorative interventions. This process is more than likely aided by the continuous clearing of IAPs by WfW as this acts to deplete alien seed banks and maintain IAPs at acceptable and manageable levels.

Keywords: Biological invasions; Ecosystem repair; Exotic plants; Diversity; Resilience; Restoration; Working for Water

1. Introduction

The introduction and establishment of invasive alien species is a global problem having severe and wide-spread consequences. Invasive alien plants (IAPs) not only negatively impact the structure and functioning of ecosystems (Vitousek, 1990; Witkowski, 1991a,b; Richardson et al., 1997; Gordon, 1998; Witkowski and Wilson, 2001), but have also been acknowledged as one of the greatest threats to global biological diversity (Coblentz, 1990; Rubec and Ledd, 1996), with numerous studies reporting negative effects of IAPs on the diversity of communities (Richardson et al., 1989, 1997; Vitousek, 1990; Pyšek and Pyšek, 1995; Dunbar and Facelli, 1999). Although diversity has various ecological definitions, in this study it refers to "the variety and abundance of species in a defined unit of study" and incorporates measures of both species richness and evenness of distribution of species (Magurran, 2004).

When considering the detrimental impacts that IAPs can have, it is not surprising that management of IAPs and restoration of ecosystems impacted by IAPs have become priorities to conservation managers worldwide (Byers et al., 2002). South Africa faces a great challenge in managing IAPs, an issue that has received much attention (Richardson and Van Wilgen, 2004). In 1995, the Department of Water Affairs and Forestry launched the "Working for Water" programme (WfW), with the primary goal of securing scarce water resources, by coordinating and conducting active clearing of IAPs across the country, while simultaneously addressing poverty alleviation through job creation (Van Wilgen et al., 1998). Clearing of IAPs is, however, a continual and complex challenge (Manchester and Bullock, 2000), and cleared areas often experience further invasion or

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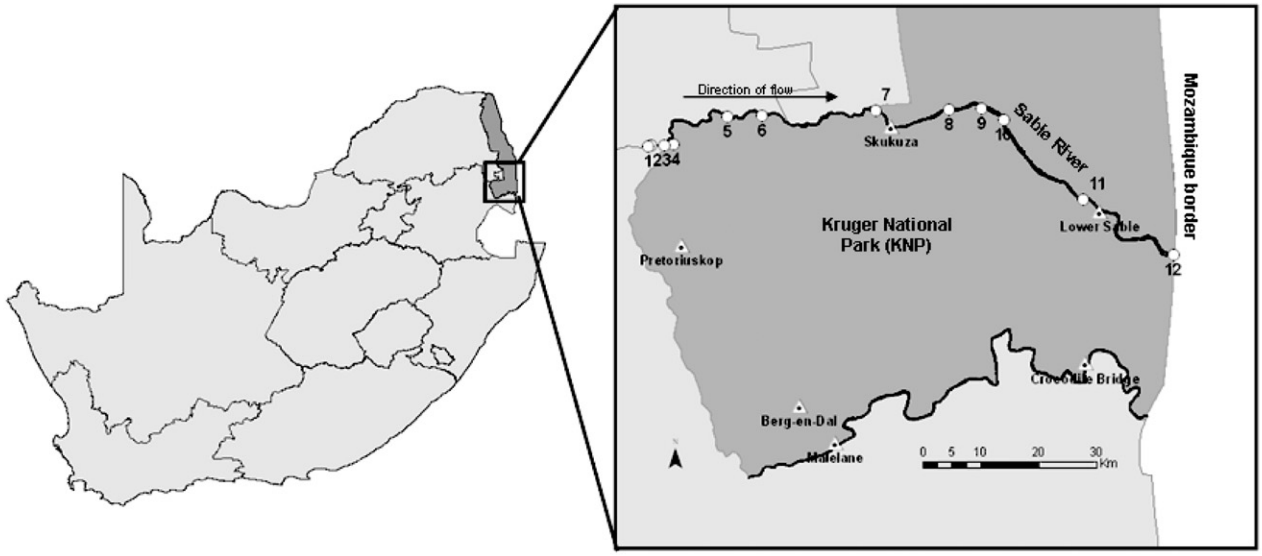

Fig. 1. Map of the Southern section of the Kruger National Park. Transects span the Sabie River and were divided into three zones according to location and propagule pressure. Zone 1: transects 1–3, outside the KNP; Zone 2: transects 4–8, in close proximity to the boundary (transect 8 is situated after Skukuza rest camp which is a propagule source) and Zone 3: transects 9–12, within the confines of the park extending to the Mozambique border.

other secondary problems (Holmes et al., 2000; Holmes, 2001; Beater et al., 2008-this issue). Regrowth by indigenous vegetation is essential to minimise the possibility of further problems and to allow ecosystem recovery to ultimately occur. While in some areas this may take place without further management intervention, in others, active maintenance and restoration can sometimes be necessary (D'Antonio and Meyerson, 2002; Galatowitsch and Richardson, 2004). Post-clearance monitoring is crucial to assess levels of post-clearance ecosystem recovery and to determine if further management is needed. However this monitoring is rarely performed and in general, sites cleared by WfW are often just left in the hope that indigenous revegetation will occur without further management intervention (Galatowitsch and Richardson, 2004).

In the Kruger National Park (KNP), South Africa, invasive alien species have been declared one of the greatest threats to biodiversity, with riparian zones being the most severely invaded systems (Foxcroft and Richardson, 2003; Foxcroft et al., 2007). Riparian ecosystems are acknowledged to be highly prone to IAP invasions due to the dynamic nature of rivers as well as the efficient ability of rivers to transport and disperse alien propagules (Thebaud and Debussche, 1991; Pyšek and Prach, 1993; Johansson et al., 1996; Tickner et al., 2001). Once present in a catchment, many of these IAP species can exploit opportunities provided by both natural and anthropogenic disturbances that are known to play a large role in determining patterns of riparian vegetation (Richardson et al., 2007). These disturbances include those linked to hydrology (flooding, sedimentation), fire, herbivory and even disturbances associated with IAP clearing (Tang and Montgomery, 1995; Naiman and Décamps, 1997; Parker-Allie et al., 2004; Richardson et al., 2007; Witkowski and Garner, 2008-this issue).

To aid in the management of IAPs, the WfW programme was first launched in the KNP in 1997, and has since become a major component of IAP management, executing annual clearing operations in selected areas. Despite this setting providing an excellent opportunity to assess impacts of IAPs and their clearing on plant community diversity and initial vegetation succession in riparian areas subsequent to clearing, very little monitoring has taken place. Investigating the impacts of and recovery from IAP invasions in such an area with relatively low anthropogenic disturbance, which should be less invaded, should provide indications of benchmark targets for similar vegetation in other areas of land-use. It should also provide a realistic test to assess to what extent natural revegetation actually occurs, subsequent to clearing of IAPs. If revegetation were not to occur in this relatively well-managed ecosystem with low anthropogenic disturbance, it definitely cannot be expected to occur in highly transformed or degraded areas. Thus, the aims of this study were to (a) assess the plant diversity of sites along the riparian zone of

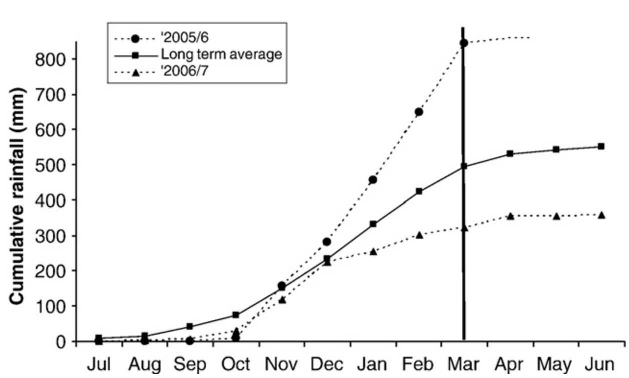

Fig. 2. Cumulative rainfall (mm) at Skukuza weather station from the beginning of the "annual climatic year" (July). The dotted lines represent the 2005/6 and 2006/7 rainfall seasons, while the solid line represents the long term average over 76 years. Vegetation sampling occurred in March, indicated by the bold solid bar.

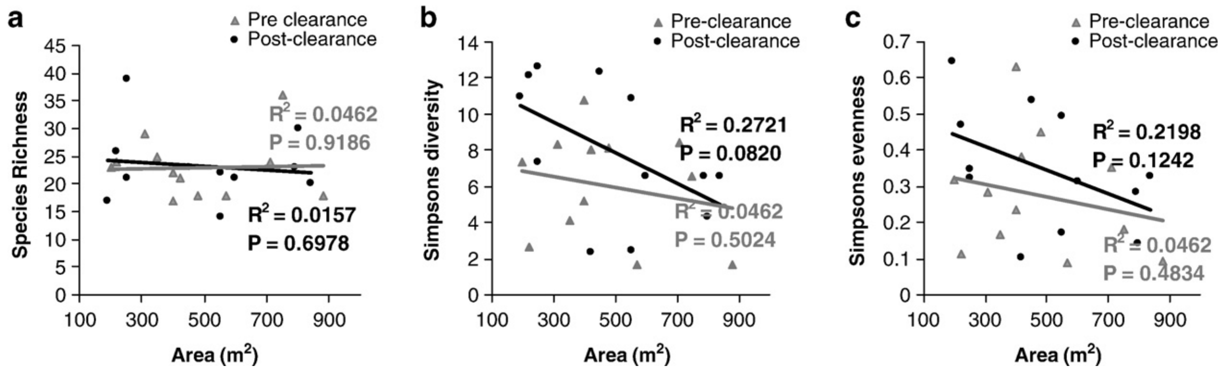

Fig. 3. Species richness (a), Simpson's diversity (b), and Simpson's evenness (c) as a function of transect area (m^2) for pre-(Mar 2006) and post-(Mar 2007) clearance of invasive alien plants. Fitted trend lines are linear.

the Sabie River in and adjacent to the KNP, in relation to the abundance of IAPs and (b) determine patterns of vegetation regrowth after clearing of IAPs in densely invaded sites.

2. Material and methods

2.1. Study area

This study was conducted along the Sabie River, in and adjacent to, the KNP. The Sabie River is a perennial river (Heritage et al., 1999) originating in the escarpment of the Drakensberg Mountains to the west of KNP. It flows eastwards through areas of commercial forestry, agriculture and dense rural habitation before entering the KNP and on to Mozambique (Fig. 1). The complex pattern of land-use and ownership upstream of the KNP provides a continual source of alien plant propagules into the riparian system, creating a continual challenge for the management of IAPs (Foxcroft and Richardson, 2003; Foxcroft et al., 2007; Beater et al., 2008-this issue).

The area is located in the savanna biome and is characterized by a semi-arid to subtropical climate, with hot rainy summers and mild dry winters (Venter et al., 2003). There is an increasing rainfall gradient from east to west (Venter et al., 2003), with an average annual rainfall of 450–600 mm (Van Niekerk and Heritage, 1993). Rainfall during the study period recorded at the Skukuza weather station was 70% greater than the 76 year long-term annual average rainfall in 2005/06, and 35% below in 2006/07 (Fig. 2).

The high rainfall experienced in 2005/2006 (Fig. 2) enhanced the response of IAP growth, and IAP densities were much greater than those reported on the same river in 2004 (Foxcroft et al., 2007). However IAP patterns are also influenced by the continuous clearing efforts of WfW, who have undertaken annual clearing operations for at least the last four years on the Sabie River. This annual clearance by WfW afforded the opportunity to assess the short-term response of IAP over just one season of growth, with the large disturbance of a high rainfall bout having occurred since the previous year's clearing operations. It also

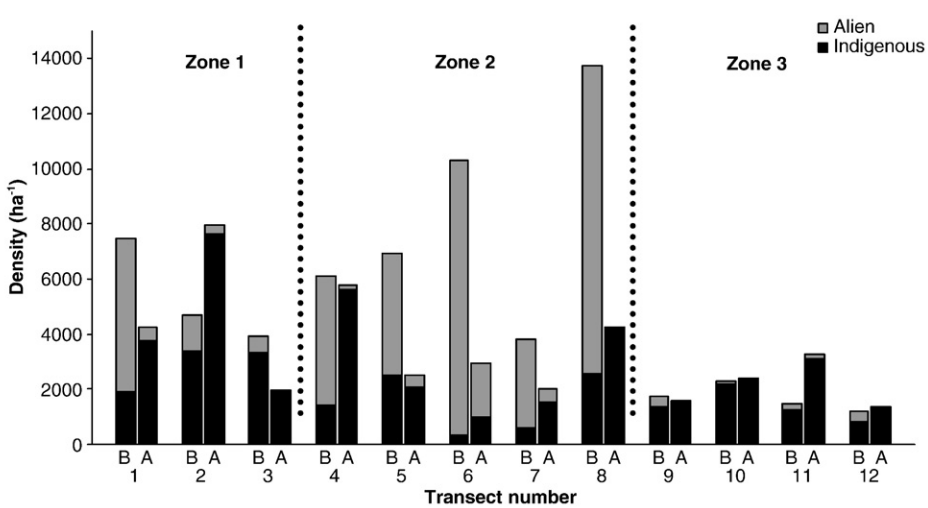

Fig. 4. Densities (per ha) of indigenous and alien vegetation (basal stem diameter > 1 cm) before (B) and after (A) the annual clearing of invasive alien plant species by the Working for Water Programme.

Table 1
Densities of alien species with a density > 5 plants/ha at any one site as well as the relative contribution of these species to the total density of all vegetation of transects with an alien density > 35% prior to the clearing of invasive alien plants

Species	Growth form	Longevity	Legal status	Density (per ha) per site					
				1	4	5	6	7	8
Acanthospermum hispidum	Herb	Annual	–		9	3			
Lantana camara	Shrub	Perennial	DW1		5			1	
Senna obtusifolia	Shrub	Annual	–	31	2	19	9		
Senna occidentalis	Shrub	Perennial	–	1	26		1		56
Tagetes minuta	Herb	Annual	–	36	32	23	5	5	1
Xanthium strumarium	Herb	Annual	DW1	3		18	78	77	24
Total percentage density of abundant alien species				72	74	62	93	83	81
Total percentage density of all invasive alien species				75	77	64	97	84	82
Percentage of total alien density				96	96	98	96	99	99

Legal status refers to regulation 15 of the Conservation of Agricultural Resources Act, 1983 (Act No. 43 of 1983).
DW1 = Declared weed 1 as described in Henderson (2001).

provided the opportunity to assess the response of the indigenous vegetation directly after clearing operations by WfW. Thus for interpretation purposes the terms before (pre-clearance) and after (post-clearance) relate only to the 2006 clearing season which targeted the high IAP densities resulting from the high rainfall season, and not to the long term clearing operations by WfW.

2.2. Vegetation sampling

Sampling took place over two periods: in March/April 2006 and in March 2007. Twelve transects were sampled along the Sabie River from Hazyview (upstream and adjacent to KNP) through the park and terminating at the Mozambique border on the eastern boundary of the park (Fig. 1). These transects were split into three zones according to their locality and hence corresponding propagule pressures: Zone 1 — transects 1–3: situated along the Sabie River outside the KNP; Zone 2 — transects 4–8: situated within the park but in close proximity to the boundary. Transect 8 was included in this zone as it is located near to the large Skukuza tourist camp and staff village, which poses a high threat for IAP invasions, mainly due to the pathway of spread of exotic species from camp and staff

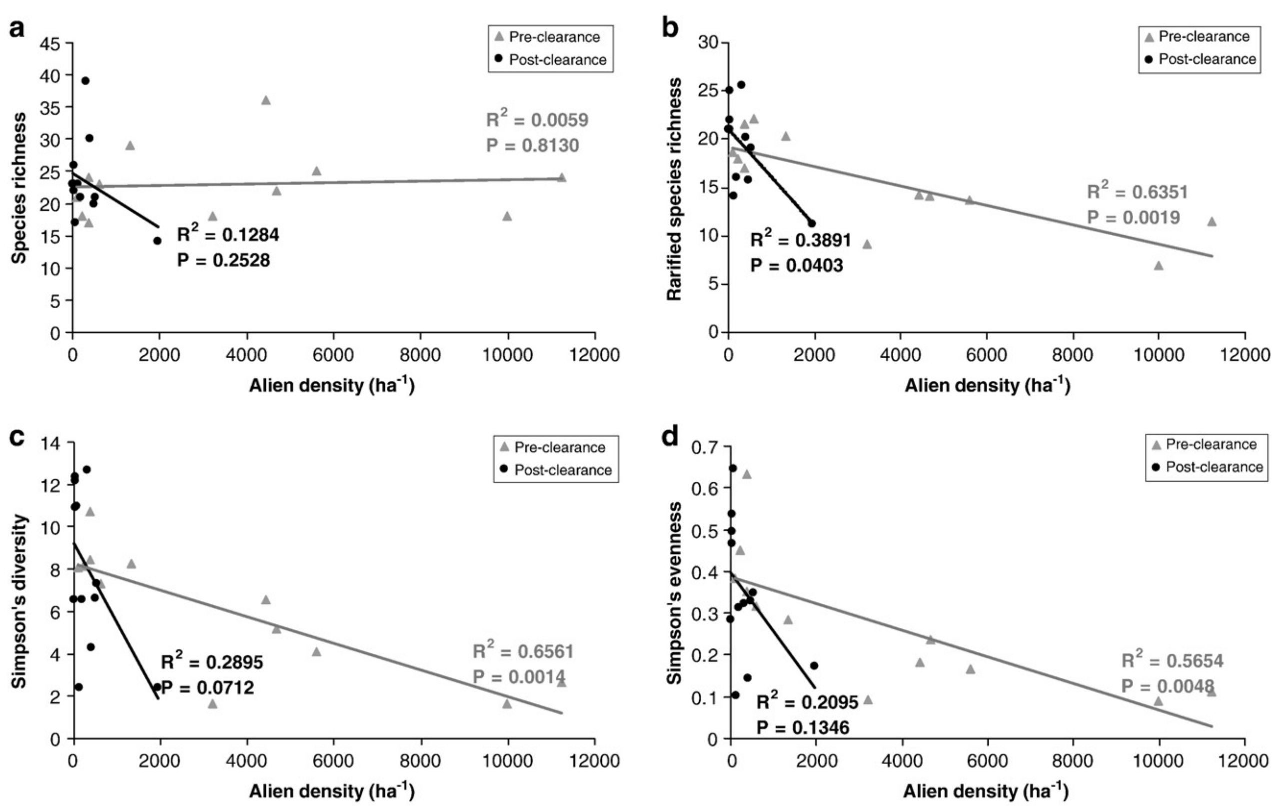

Fig. 5. Species richness (unadjusted and rarefied) (a, b), Simpson's diversity (c) and Simpson's evenness (d) as a function of alien density (per ha) before (Mar 2006) and after (Mar 2007) the seasonal clearance of invasive alien plants by Working for Water.

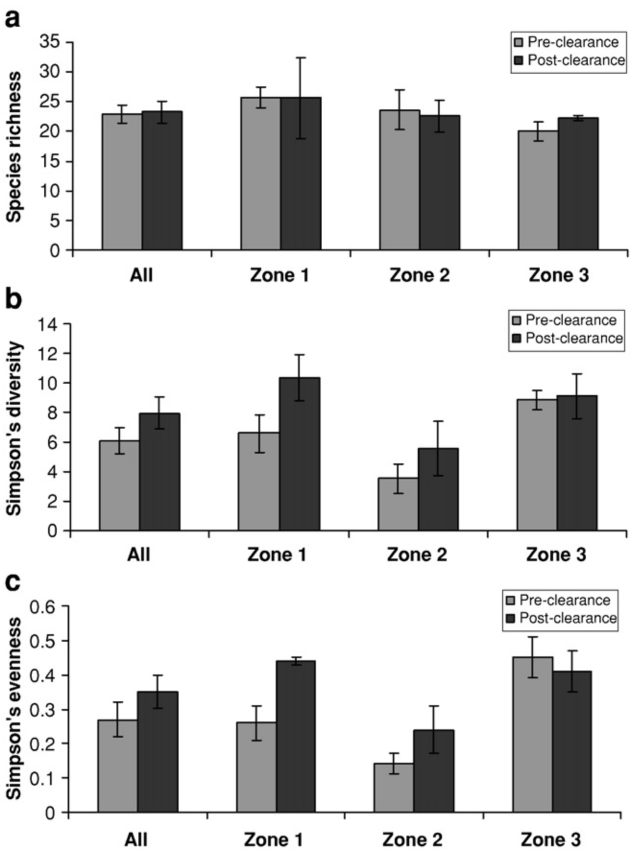

Fig. 6. Pre- and post-clearance species richness, Simpson's diversity and Simpson's evenness for all transects and each zone.

gardens (Foxcroft and Richardson, 2003); Zone 3 — transects 9–12: located along the Sabie River within the confines of the KNP extending to the Mozambique border.

Vegetation with a basal stem diameter (BSD) > 1 cm was sampled in a 10 m wide belt transect placed perpendicular to the river. This belt transect extended from the top of the macro-channel bank to the beginning of the macro-channel floor. However, due to the heterogeneous nature of the riparian zone along the 108 km stretch of the Sabie River, these transects varied in length from 20–90 m. In each transect individual plants were identified and counted, the BSD and height class were recorded and the growth forms were later classified as herb, shrub or tree according to Germishuizen and Meyer (2003).

Transect 3 was omitted from all before versus after analyses as this transect had subsequently been transformed into farm-lands by the second data collecting period and hence no "after" data could be collected for this site.

2.3. Data analysis

The following diversity indices were derived for combined alien and indigenous vegetation using Primer™ v5 (Clarke and Gorley, 2001) and utilised to assess possible area affects between transects of differing lengths and hence areas:

a) Observed species richness (S)
b) Rarefied species richness ($n = 100$): the expected number of species for a given number of randomly sampled individuals (McCabe and Gotelli, 2000).
c) Simpson's diversity index (D) and reciprocal ($1/D$).
d) Simpson's evenness index ($E_{1/D}$).

Densities of alien and indigenous vegetation were assessed before and after the annual clearing by WfW and tested for significant differences over time using Wilcoxon matched pairs tests in Statistica 6.1 (StatSoft, 2004). Mann−Whitney U-tests were used to assess differences in before clearance alien densities between the three zones along the River. Diversity indices were assessed across the three zones before and after the annual clearing by WfW and were also plotted against alien densities to investigate potential effects of alien intensity on vegetation diversity.

Indigenous densities categorised into growth form were considered before and after the annual clearing of IAPs. The densities of species that increased in abundance over time were square-root transformed and the percentage contribution of the

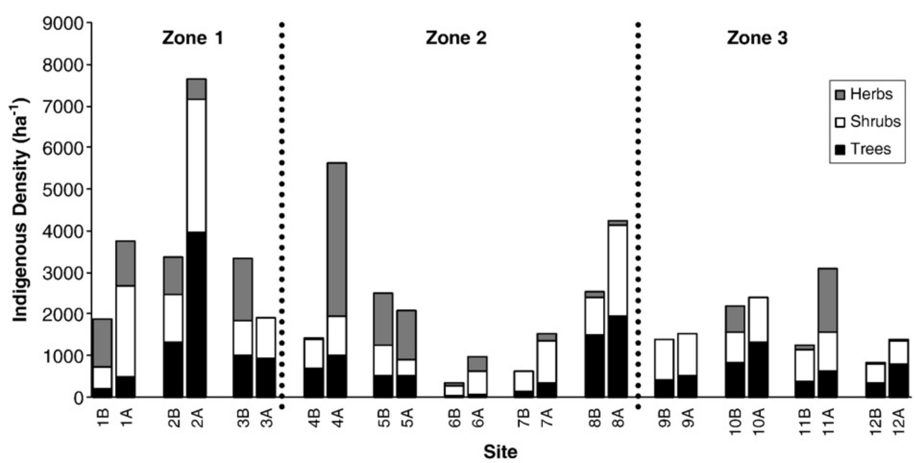

Fig. 7. Density (per ha) of indigenous vegetation before and after the seasonal clearing by Working for Water. Densities are divided into three growth forms: trees, shrubs and herbs. *Data could not be collected at transect 3 after clearing of invasive alien plants as this site had been transformed into farm lands. Thus post-clearance densities are derived from an intermediate data set and were excluded from interpretation.

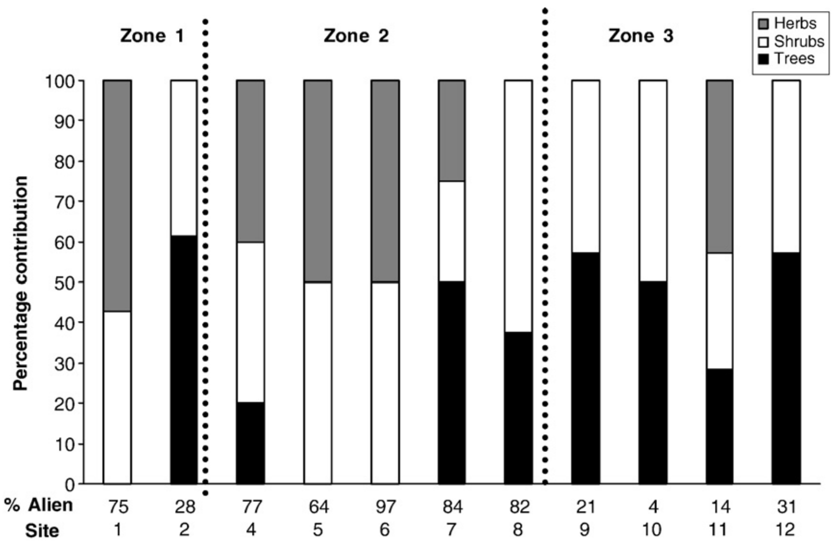

Fig. 8. Percentage contribution of the growth forms of species that increased after clearing, contributing to 70% of the observed change post-clearance of invasive alien plants.

species responsible for 70% of the variation within a site before and after clearing of IAPs was calculated. A 70% cut off was used to highlight the species that contributed most to the observed changes. Indigenous herbaceous plant densities that increased over time were tested for a significant difference between heavily- versus lighty-invaded transects using Mann−Whitney *U*-tests.

3. Results

3.1. Effects of variation in transect length (area)

Species richness is expected to increase as area increases. However, as transect areas increase, this expected relationship is not observed, either before (2006) or after clearance (2007). There is no relationship between transect area and species richness ($P>0.05$) (Fig. 3a) and, unexpectedly, both species diversity (Fig. 3b) and evenness (Fig. 3c) decrease slightly as transect area increases ($P>0.05$). These results suggest that macro-channel banks along the lower Sabie River are comparable regardless of transect length. This may be of importance when considering future sampling methods as plots of a fixed size may misrepresent the full extent of riparian macro-channel banks, which can vary dramatically down the length of the river, and hence underestimate diversity. Thus regardless of the differing lengths, and hence areas across the sites, data were still considered comparable due to the negligible area effects.

3.2. Densities of invasive alien plants before and after annual clearing

The density of IAPs before (B) clearing by WfW outside the KNP (Zone 1: transects 1–3) was slightly lower than for transects within the park in Zone 2 (transects 4–8) although differences were not significant ($P=0.18$). Density was lowest in transects further downstream towards the Mozambique border (Zone 3: transects 9–12) ($P=0.014$) as would be expected with an increasing distance away from the major propagule sources upstream of the western boundary. Densities of IAPs (plants/ha) after clearing (343 ± 156), were significantly reduced ($P=0.002$) relative to before clearance levels (3508 ± 1113), with a mean IAP reduction of $80 \pm 6\%$ (Fig. 4).

Prior to clearing, species that contributed most to the alien plant density of heavily-invaded transects were *Acanthospermum hispidium* (DC.), *Lantana camara* (L.), *Senna obtusifolia* (L.), *Senna occidentalis* (L.), *Tagetes minuta* (L.) and *Xanthium strumarium* (L.). These six species contributed between 62–93% of all vegetation density at the previously highly-invaded transects (transects 1, 4–8) (Table 1).

3.3. Effects of invasive alien plant density on community diversity

When investigating the effects of IAPs on community diversity, there was no relationship between alien density and species richness ($P>0.05$) (Fig. 5a). However when species

Table 2
Total percentage contribution to change (600%) of the three highest indigenous species per site that increased in the previously densely invaded sites (>50% density alien invasion)

Species	Growth Form	Longevity	Transect number						Total
			1	4	5	6	7	8	
Sida cordifolia	Herb	Annual		49	48	31	19		146
Phyllanthus reticulatus	Shrub	Perennial	17	9				10	36
Acacia schweinfurthii	Shrub	Perennial			9		14		23
Leonotis intermedia	Shrub	Perennial				21			21
Pluchea dioscoridis	Shrub	Perennial				17			17
Pavetta catophyla	Shrub	Perennial						15	15
Triumfetta rhomboidea	Herb	Annual	14						14
Crotolaria capensis	Shrub	Perennial	14						14
Acacia robusta	Tree	Perennial					9		9
Waltheria indica	Herb	Annual			9				9
Pyrostria hystrix	Shrub	Perennial						9	9
Flueggea virosa ssp. *virosa*	Shrub	Perennial		6					6

richness was rarefied to $n=100$ for comparison across transects, it decreased as alien density increased ($P<0.05$) (Fig. 5b). Additionally, alpha diversity and evenness decreased as alien density increased (pre-clearance data: $P<0.05$) (Fig. 5c,d). These results occurred irrespective of whether densities were calculated on an absolute or relative basis (Morris, 2008).

When considering changes in diversity measures before and after clearing, in each zone and overall, there were no change in species richness (Fig. 6a). Alpha diversity and evenness remained unchanged in zone 3, which was mostly unaffected by IAP invasions. However in zone 1 and 2, there was a trend for both alpha diversity and evenness to increase despite the reduced rainfall received in 2006/07 (Fig. 6b,c). This suggests that the drastic reduction of IAPs in these zones may have lead to this initial increase in these diversity measures.

3.4. Response of indigenous vegetation to the seasonal clearing of invasive alien plants

Overall, densities of indigenous species increased after the clearing of IAPs (Fig. 7) ($P=0.02$) with both tree and shrub growth forms increasing significantly after clearing ($P=0.04$, $P=0.015$, respectively). Interestingly, the species that increased in previously densely-invaded transects (alien density > 50%), were mostly herbaceous ($P=0.067$). Species that increased in the less invaded transects, however, were tree species ($P=0.022$) (Fig. 8), as would be expected in relatively undisturbed areas experiencing normal recruitment.

The herbaceous species that contributed the most to the increase in indigenous plant abundance after clearing were *Sida cordifolia*, *Triumfetta rhomboidea* and *Waltheria indica*; while *Acacia schweinfurthii* var. *schweinfurthii*, *Leonotis intermedia* and *Phyllanthus reticulatus* var. *reticulatus* contributed to the greatest increase in shrub abundance, and *Acacia robusta* contributed to the increase in tree species abundance (Table 2). This supports the use of *A. robusta*, which regenerates relatively easily from seed (Witkowski, E.T.F., unpublished) for restoration planting in riparian areas within this ecoregion (Holmes et al., 2008-this issue).

4. Discussion

4.1. Changes in alien densities and community diversities

Prior to clearing by WfW (2006), transects had IAP densities of up to 97%. These high IAP densities appeared to have a negative impact on community diversity (Fig. 5), which is congruous with results of numerous other studies (e.g. Pyšek and Pyšek, 1995; Holmes et al., 2000). After the reduction in IAP density, there was a notable corresponding increase in the alpha diversity and evenness of vegetation in the previously densely-invaded sites (Fig. 6). The major contribution to the high IAP densities was from annual or short-lived perennial species such as *X. strumarium* (L.), *S. obtusifolia* (L.), *S. occidentalis* (L.) and *T. minuta* (L.). The short longevity of these species may result in these plants dying off naturally at the end of the annual growing season, making clearing seem redundant. However clearing of these species reduces both reseeding and the shading out of regenerating indigenous herbaceous species, and thus acts against the annual reinvasion of herbaceous IAP species. Perhaps clearing the densely-invaded areas before these IAPs have the opportunity to set seed, would minimise the perpetuation of these herbaceous IAPs and reduce the overall management effort necessary to control these species in the long term.

4.2. Response of indigenous vegetation to the seasonal clearing of invasive alien plants

Herbaceous growth forms increased in response to clearing of IAPs in transects that were previously densely-invaded. This is congruent with the notion that recovery from plant invasion is observed quickest in changes to herbaceous diversity and abundance, followed by shrubs and trees (Mentis and Ellery, 1994; Connel and Slayter, 1977). The short time span of this study, as well as the compounded effects of annual clearing, renders it difficult to fully explore successional changes in the indigenous vegetation. However, the important point with regards to the recovery of the system after clearing, is that recolonisation of vegetation is largely by indigenous species rather than the undesirable situation of reinvasion by the same or other exotic species, as was the case further up in the catchment (Beater et al., 2008-this issue; Witkowski and Garner, 2008-this issue).Vegetative ground cover of indigenous vegetation also increased after the clearing of IAPs mostly due to an increase in grass cover (Morris, 2008).

The high levels of observed overall indigenous regrowth indicate that the system shows a relatively high level of resilience to disturbance by IAPs. Resilience is defined as the ability of an ecosystem to return to its former state following a disturbance or stress (Wali, 1999). Most riparian species are inherently resilient due to frequent and intense disturbance (Richardson et al., 2007) and have dispersal and establishment strategies, such as the ability to colonise bare sediments and aggressive clonal growth that allow for rapid recovery after a disturbance event (Naiman and Décamps, 1997).

The continuous management and clearing of IAPs by WfW is an important factor that facilitates this resilience in the system, as the repetitive clearing depletes alien seed banks and maintains IAPs at acceptable levels that are relatively easy to manage. Acceptable levels of IAPs are based upon the KNP management objectives which incorporate the use of "Thresholds of Potential Concerns" (TPCs) concerning the distribution, density and rate of spread of IAPs (Foxcroft and Richardson, 2003). Thus the WfW operations ensure that stands of IAPs are present for short periods. This probably improves the chances of natural post-clearing recovery occurring, as the longer an invader has been present, the more dense and widespread its seed bank will become (Witkowski and Wilson, 2001), and the greater its contribution to the attrition of native seed banks and its impact on indigenous plant propagule input (Holmes and Cowling, 1997a,b).

4.3. Spatial variation in alien densities

Densities of IAPs were significantly higher in the first two zones prior to their clearing. This is probably attributable to the combination of two factors: the aforementioned above average rainfall and the higher propagule pressure. The Sabie River flows through areas of varying land-use including areas of commercial forestry and dense rural habitation even after entering the KNP, as the river acts as a boundary for some distance (Fig. 1, transects 4–7) (Foxcroft et al., 2007; Beater et al., 2008-this issue). This continuous interface with human disturbance allows multiple opportunities for introduction of alien propagules into the riparian corridor, resulting in recurring germination and establishment of alien plants (Richardson et al., 2007; Witkowski and Garner, 2008-this issue). Interestingly, transect 8, situated downstream of Skukuza rest camp, had the highest alien density even though it is not on the park boundary. This supports the notion that the gardens of rest camps and staff villages act as major pathways for alien invasions (Foxcroft and Richardson, 2003). Further downstream within the KNP, there are very few, if any, sources of alien propagules besides those originating from alien plants in adjacent reaches and correspondingly, densities of IAPs are considerably lower.

Transects outside the KNP tended to have lower densities of IAPs than those of zone 2 within the park, which is rather surprising as one would expect this area to be subjected to greater human impacts and hence to be more disturbed. The only transect in keeping with this, appearing to be highly disturbed, was transect 1, which was frequently used by both humans and livestock (T. Morris, pers. obs.), and correspondingly supported a relatively high density of IAPs. The other two transects were relatively unutilised, probably due to their inaccessibility and steeper gradients and in contrast supported high densities of indigenous vegetation, and had high alpha diversity and species richness. Thus, the only variable in common between the heavily-invaded sites both within and adjacent to the park was the presence of faunal disturbance. Riparian zones within the KNP are heavily utilised by a range of large herbivore species who create a further disturbance and perhaps also provide additional vectors for propagule dispersal along the riparian zone by spreading propagules while foraging or by spreading those that attach to their fur (Hood and Naiman, 2000).

4.4. Role of disturbance in the dynamics between indigenous and exotic plant growth

Natural and anthropogenic disturbances, such as herbivory, fire, hydrological processes and even disturbances created by IAP mitigation, play a large role in determining patterns of riparian vegetation (Witkowski and O'Connor, 1996; Richardson et al., 2007). In the KNP where there is an increased use of the riparian zone by mega-herbivores, herbivory may play an important but unexplored disturbance role. On the other hand, fire is generally considered relatively uncommon in the riparian zones of higher order streams in the KNP (Pettit and Naiman, 2007a), such as the Sabie River. This is largely due to the high levels of moisture and lower fuel loads in comparison to uplands (Dwire and Kauffman, 2003). Additionally, tourists roads are situated along almost the entire length of the southern bank of the Sabie River, where study transects were situated. These roads may be acting as additional "fire-breaks", unintentionally preventing fires spreading from upland areas into the riparian zone. Thus fire in all likelihood does not play a major role in determining vegetation patterns in the sampled areas. However, the role of fire can become more important when it occurs as a result of, or in conjunction with, other disturbances such as floods.

Flooding and water levels play a large role in characterising riparian vegetation (Van Coller et al., 2000). Opportunities for recruitment and colonisation occur mostly after floods when new patches are exposed either due to the removal of vegetation or through sediment deposition (Richardson et al., 2007). In February 2000, when severe flooding occurred in the KNP region, the Sabie River flood peaked between 3000 m^3/s and 7000 m^3/s at different points along the river (Heritage et al., 2001). When compared to the typical wet season base flow discharges of 15–20 m^3/s, it is clear that this flood was of enormous magnitude. The estimated return interval of the flood was 90–200 years, depending on the position in the catchment (Smithers et al., 2001) and was considered a large infrequent disturbance (LID). This LID reduced the extent of tree, shrub, reed and herbaceous patches, and increased the extent of sand, rock and water patches on the Sabie River within the KNP (Parsons et al., 2006), thus opening many new areas for colonisation. In this case, it was expected that increased colonisation of exotic species would occur due to the disproportionate propagule input into the system. Large amounts of IAP propagules would have washed down from the highly disturbed and transformed areas of the upper Sabie River catchment (Beater et al., 2008-this issue), whereas indigenous propagule pressure would be mostly reliant on residual indigenous vegetation, which was relatively sparse after the 2000 flood (Parsons et al., 2005). Leroy (2003) confirmed this and showed an increase in alien woody and herbaceous species along the Sabie River directly after the 2000 flood relative to preflood (1997) on the same transects.

Before the 2000 flood, herbaceous IAP species were not a strong focus of IAP management, as they were considered more difficult to control manually and were expected to eventually be reduced naturally over time as competition with native species increased. Competition between alien and native species tends to increase as the native community matures during the course of succession. However due to the highly dynamic nature and the frequent disturbances experienced along the riparian zone, typical succession seldom occurs, giving IAPs a continual competitive advantage in this largely non-equilibrium system. In this light, the effective clearing of both herbaceous and woody species executed by WfW may play an important role in aiding both the physical and temporal recovery of indigenous vegetation after the LID, by reducing the competitive effects of IAP.

LIDs may have long-lasting influences on ecosystems (Foster et al., 1998) and can also alter other important disturbance regimes such as fire. For instance, large woody piles deposited after a flood of this magnitude increase fuel loads and therefore the susceptibility of the riparian zone to fire (Dwire and Kauffman, 2003). Pettit and Naiman (2007b) illustrated that fires enhanced by these large woody piles had a significant initial effect on Sabie River vegetation and showed how fire could alter pathways of succession after floods by causing the destruction of surviving and regenerating vegetation. Thus the dynamics of IAP growth and indigenous vegetation regrowth may still be greatly compounded by the February 2000 floods.

Lastly, clearing operations can also be a source of disturbance whether in the form of physical disturbance, disturbances to ecosystem processes (e.g. erosion) or negative effects on non-target species (D'Antonio and Meyerson, 2002; Galatowitsch and Richardson, 2004; Parker-Allie et al., 2004). However, due to the dense, largely mono-specific stands of invasion along the Sabie River, as well as the highly-specific and largely manual rather than chemical practices utilised by the WfW teams, negative impacts of clearing on native vegetation appeared to be fairly minimal (T. Morris, pers. obs.) compared to upstream in the catchment (Beater et al., 2008-this issue).

In 2004, less than 6% of the total plant abundance was composed of alien species, which may have indicated the effectiveness of the ongoing clearing programme (Foxcroft et al., 2008-this issue), especially in light of the increased levels recorded directly after the large flood disturbance in 2000. However, after just one season of above average rainfall in 2006, alien densities increased up to 97% in isolated areas. Thus it is important for management to realise that the responses of exotic and indigenous vegetation can be complex and highly heterogeneous in both space and time and hence management regimes should correspondingly be fairly flexible. This is of utmost importance when dealing with invasions associated with large disturbances, such as a flood or an escalated rainfall season, so that IAPs infestations can be dealt with effectively and without delay so that IAPs can be maintained at acceptable and manageable levels.

In areas that are relatively undisturbed by human activity, such as reserves or conservation areas, revegetation and recovery of indigenous vegetation after the clearing of IAPs should occur without further management steps being necessary. However, continuous management of IAPs plays a vital role in management, boosting the resilience of the system, and making rapid recovery viable. Over a short term, monitoring the response of both alien and indigenous vegetation to clearing of IAPs has provided several worthy insights. However, long term monitoring is crucial to build upon our understanding of the role of seed banks, environmental influences and disturbances in perpetuating IAP invasions and hence allowing us to advance and optimise management operations accordingly.

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